VEGETATIVE REPRODUCTION IN *DROSERA PELTATA* AND *D. AURICULATA.*

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(Plate viii; thirty-four Text-figures.)

Introduction.

Drosera peltata Sm. and *Drosera auriculata* Backh. are winter herbs common in the Sydney district. They perennate by means of small, more or less spherical tubers, situated at the base of underground stems.

These two species belong to the subgenus *Ergaleium* Planch. of the Droseraceae. Bentham (1864) follows the older classification of the Droseraceae, in which the genus *Drosera* is divided into two subgenera, *Rorella* and *Ergaleium*, distinguished by means of their types of perennating organs. In the former, the short stock or stem forms, at its upper end, the winter bud which will develop in the following year. In *Ergaleium*, on the other hand, the plant is characterized by the production of a tuber at some distance below the surface of the ground. It is from this tuber that the bud develops which will form the plant in the following season.

Planchon (1848), in his monograph on the Droseraceae, divides the genus *Drosera* into thirteen sections, on account of some anomalous species. Drude (1891, in Engler and Prantl) divides it into five subgenera. Both authors retain the section *Ergaleium* on account of the characteristic method of vegetative reproduction shown by all its members.

Relatively little work appears to have been done on this section of the Droseraceae, and as both *D. peltata* and *D. auriculata* are abundant in the Sydney district, it was thought that a study of the developmental history of their underground parts, and their relationship to their environment, might prove of interest.

According to Ewart (1930), *D. peltata* and *D. auriculata* are both found throughout the Eastern States of Australia, viz., Queensland, New South Wales, Victoria and Tasmania, and also South Australia. *D. auriculata* is in addition recorded from New Zealand.

In the Sydney district, *D. peltata* and *D. auriculata* are abundant on the sandy soils, but both species are also frequently found on the heavier clay soils. *D. peltata* is common on the margins of peaty swamps, especially when the surrounding vegetation is not very dense. Soil moisture appears to be the chief factor governing their ecological distribution. In well drained areas, such as on the tops of sandstone ridges, they are only found in the autumn, winter, and early spring, while the soil still retains considerable moisture, and soon disappear when the warmer weather causes the surface to dry. They are only plentiful during the cooler months of the year. *D. peltata* is usually the first to appear, in moist sheltered places; *D. auriculata* occurs rather later, and apparently

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requires an even moister habitat for its best development. The plants are capable of passing through their active phase in a few weeks, and may flower and fruit and die down to the ground in a short period if the moisture conditions become unfavourable.

D. peltata and D. auriculata are very alike in their habit and vegetative characters. The leafy aerial stem is erect, somewhat flexuose if very long, averaging about 20 to 30 cm. in height. The leaves at ground level may be reduced to short or occasionally fairly long, linear scales, or else they may form a rosette of leaves with orbicular or almost reniform laminae and distinct petioles. The scattered foliage leaves above these are peltate or broadly crescent-shaped on slender petioles.

In D. auriculata the foliage is always of a pale green colour, while in D. peltata the leaves vary from a similar colour to a quite deep red.

The stem has an underground region varying from less than 1 cm. to 9 or 10 cm. in length, and is terminated by a small, more or less spherical tuber. In D. peltata this is always of a bright red colour; in D. auriculata it is typically yellowish.

In the investigation here reported, the annual development of the tubers has been considered, together with the relationship existing between habitat and the depth of the tuber below the surface of the ground.

An accessory method of vegetative reproduction is also described, both D. peltata and D. auriculata exhibiting the phenomenon of epiphyllous budding. These leaf-borne buds have been studied with a view to ascertaining the precise way in which they originate on the lamina, and the physiological factors influencing their production.

Tuber Formation.

The morphology of the underground parts has been described in D. gracilis by Planchon (1848). His observations were based on herbarium and preserved material, which proved inadequate for the determination of several interesting points, and he directed attention to a number of questions which he left to be elucidated by future research on living material.

Diels (1906a) figures the underground parts of D. microphylla, D. heterophylla, D. rosulata, D. squamosa, and D. bulbosa, but gives no description of their developmental history.

Morrison (1905, 1907) examined the underground parts of D. bulbigena, D. calycina, D. stolonifera, and D. erythrorhiza. These species have not been examined by the writer. Since, however, several observations which have been made on D. peltata and D. auriculata differ considerably from the description given by Morrison, and since he did not give any details or figures of developmental stages, it has been thought advisable to give an account of the development of the underground parts from the time of the germination of the seed.

Lubbock (1892) gives an account of germination in D. rotundifolia and D. binata in which the cotyledons are epigeal. D. peltata and D. auriculata differ from these in that the cotyledons are retained within the seed coat.

Rendle (1925) states that in those species of Drosera in which germination has been studied, the primary root is absent, its place being taken by a protocorm-like development of the hypocotyl, bearing long attaching hairs. This protocorm is a temporary structure, and is later replaced by adventitious roots developed from

the stem. This condition differs entirely from that which obtains in *D. peltata* and *D. auriculata*.

Seeds of both species germinated readily in the laboratory on moist filter paper in Petri dishes. The seedlings commenced to appear after about 14 days. Observations on the early stages of germination and on the development of the seedling were made from these plants, but the development of the tuber in the young plant was studied from plants found growing under natural conditions.

The radicle emerges from the seed first, and grows downwards to form a short primary root (Text-fig. 1). This never attains any considerable size and only functions for the first season in the life of the plant. The plumule appears soon afterwards (Text-fig. 2), and the developing seedling remains attached to the seed by the two cotyledons, which never entirely emerge from the testa.

Text-figure 3 shows a later stage in the germination of the seed of *D. peltata*. The stem has elongated considerably, and the foliage leaves have unfolded, exposing the glandular hairs. The leaves are always small during the first season's growth, and are orbicular in shape. Root hairs develop on the radicle, which remains relatively short. In *D. peltata* a rosette of leaves is not formed in the seedling, the internodes being relatively long.

After the shoot has ascended for a greater or less distance, a bud (D, Text-fig. 4) in the axil of one of the lower foliage leaves becomes active, grows out and turns downwards. This bud forms a whitish coloured descending stolon, or 'dropper', which is destined to bear the first perennating tuber at its apex. For convenience, this descending stolon will be referred to throughout this paper as the 'dropper'.

The 'dropper' is morphologically a stem, as was pointed out by Planchon (1848), and bears small scale leaves. In both *D. peltata* and *D. auriculata* the colourless scale leaves present on the 'dropper' are very much smaller than those figured for *D. gracilis* by Planchon. They may be seen more clearly on older and larger plants (see Text-figs. 9 and 11). The scale leaves are homologous with true foliage leaves, and are potentially capable of developing into them, as is shown by an examination of some unusual specimens to be described later.

The 'dropper' may penetrate about 1 cm. into the soil during the first season, and the first tuber is formed at its end. During this process the growing point becomes inverted, because of the cessation of growth on one side of the 'dropper', while the other side increases in size. The parenchymatous tissue then becomes enlarged and packed with food material in the form of starch grains. Fat also occurs in the epidermis and in a few cells associated with the vascular bundles.

The dormant apical bud which is now directed upwards can be detected with a lens as a cluster of minute scale leaves surrounding the growing point. Other scale leaves occur on the surface of the tuber and are clearly seen in section (Text-fig. 6), but are usually inconspicuous macroscopically.

A longitudinal section through the apex of a 'dropper' (Text-fig. 5) shows the apical meristem surrounded by leaf initials. A vascular bundle (L) passes from the vascular tissue (V) of the stem to the base of each scale leaf, but does not pass into the leaf tissue itself. A slightly unequal growth on opposite sides of the stem can already be noticed.

A longitudinal section of a young tuber formed at the apex of a 'dropper' (Text-fig. 6) shows the apical bud now pointing directly upwards, and the vascular bundles forming a loop in the ground tissue. Further enlargement of the ground
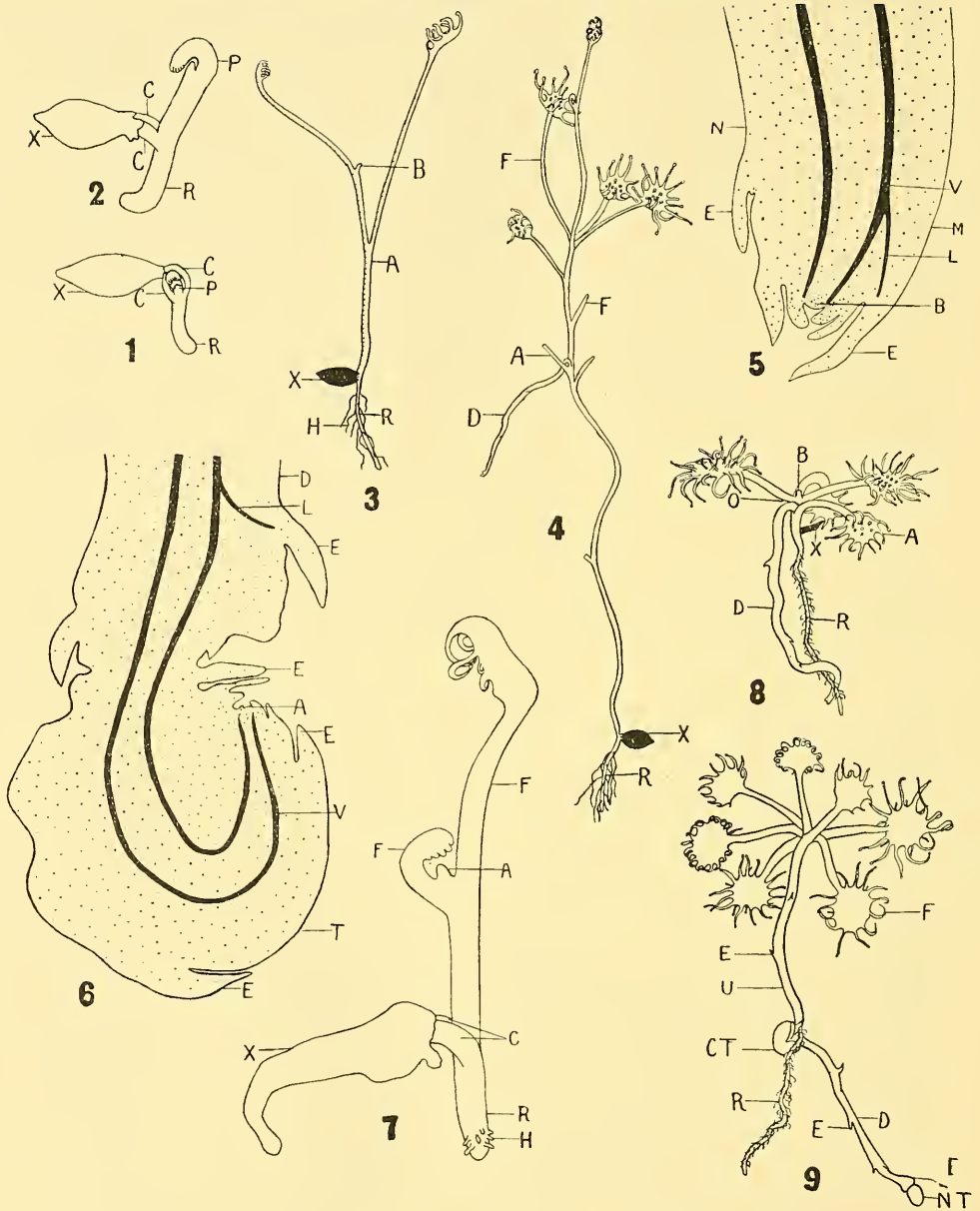
Text-fig. 1.—A very young seedling of *D. peltata*. R, radicle; P, plumule; C, cotyledons; X, testa. × 34.

Text-fig. 2.—A young seedling of *D. peltata*. R, primary root; P, plumule; C, cotyledons; X, testa. × 32.

Text-fig. 3.—A seedling of *D. peltata*. R, root; H, root hairs; X, testa; A, aerial stem; B, apical bud. × 9·5.

Text-fig. 4.—A seedling of *D. peltata* with a 'dropper'. R, root; X, testa; D, 'dropper' arising in the axil of the foliage leaf (A); F, foliage leaves. × 10.

tissue takes place until the diameter of the tuber is many times that of the 'dropper'.

Rendle (1925, p. 193) states that in the subgenus *Ergaleium*, the 'bulb' "consists of very closely united leaves of which only the tips are free, and form a peristome-like crown surrounding the base of the hypogeal caulome". I have not seen this condition in any of the specimens examined. The tuber has always been found to be a solid mass of ground tissue bearing small scale leaves.

The tuber formed during the first season is very small, frequently only about 1 mm. in diameter. At the end of the growing season, the aerial and underground stems die, and the tuber remains in the dormant state.

The development of the seedling in *D. auriculata* follows a similar course. In a young seedling of *D. auriculata* (Text-fig. 7) the tips of the cotyledon are again seen to be retained within the seed coat. At a later stage (Text-fig. 8) the shoot differs from that in *D. peltata* in that the leaves are arranged in a rosette, the internodes remaining very short. The radicle (R) forms a short unbranched root covered with numerous long root hairs. The 'dropper' (D) arises in the axil of one of the lower leaves. The formation of the tuber at the end of this 'dropper' and the subsequent development of the underground organs is similar to that in *D. peltata*.

At the commencement of the next growing season the apical bud of the tuber grows up through the soil, and on reaching the surface, it forms a rosette of leaves. The arrangement in a rosette of the first few foliage leaves, almost invariably takes place during the first few years in the life of any individual plant in both species. In an older plant this is not always the case. There may then be a small cluster of scale leaves at ground level (Text-fig. 11). At times these scale leaves may be quite long (Text-figs. 13, 15). The elongated leafy stem, at the apex of which the flowers are borne, develops above the rosette.

At this stage it will be convenient to define the terms which will be used in the description of subsequent development. That part of the stem which develops from the tuber, and which is situated below the surface of the ground, will be referred to as the underground stem (the rootstock of Morrison, 1905). The aerial stem continues the growth above the ground. The tuber from which the stem has developed, and which is therefore in the process of being exhausted, will be termed the current tuber. The term 'old tuber' will only be applied to those which have been exhausted during a previous season's growth.

Text-fig. 5.—A longitudinal section of the apex of a 'dropper'. B, apical bud; E, scale leaves; V, vascular bundle; L, leaf trace. Growth on the side M has been greater than on the side N, so that the apical bud is already slightly to one side. × 17·5.

Text-fig. 6.—A longitudinal section of a young tuber. T, tuber; D, base of 'dropper'; A, apical bud; E, scale leaves; V, vascular bundles; L, leaf trace. × 13·5.

Text-fig. 7.—A young seedling of *D. auriculata*. R, root developed from the radicle; H, root hairs; X, testa; C, cotyledons; A, apical bud; F, foliage leaves. × 12.

Text-fig. 8.—A seedling of *D. auriculata* with a 'dropper'. R, root; D, 'dropper' arising in the axil of the foliage leaf (A); X, testa; B, apical bud; O, rosette of foliage leaves. × 5.

Text-fig. 9.—A plant of *D. auriculata* in its second year. Its rosette of leaves is drawn from below. NT, new tuber; D, 'dropper'; B, swollen end of 'dropper' just above the new tuber; E, scale leaves; CT, current tuber; R, root; U, underground stem; F, foliage leaf. × 3·6.

Scale leaves occur at intervals throughout the length of the underground stem. Elongation of the underground stem or of the 'dropper' in the ground after the formation of the scale leaves, frequently causes them to appear, from a superficial examination, to point in the opposite direction to that which would be expected.

Short adventitious roots develop on the underground stem. They are most numerous immediately above the current tuber, but others occur scattered throughout its length. Diels (1906b) has pointed out in the case of *D. erythrorhiza*, that these roots arise at the base of the scale leaves, to which they appear to be attached. This observation has been confirmed for *D. peltata* and *D. auriculata*. Roots may occur either singly or in twos and threes at the leaf base (Text-fig. 11). The relatively poor development of the root system may account for the restriction of these species to rather moist localities.

The 'dropper' which is destined to bear the new tuber typically arises in the axil of a scale leaf immediately above the tuber of the current year, and penetrates more deeply into the soil. When growing in soil of moderate depth, the 'droppers' usually point vertically downwards; but in the plants which grow on rock ledges, the 'dropper' often becomes coiled and twisted, where its downward progress has been checked by contact with the hard rock. The growing point of the 'dropper' ultimately becomes inverted and swollen to form the new tuber.

Text-fig. 9 shows a plant of *D. auriculata* in its second year. The shoot arises from the apex of the current tuber (CT). It bears a laterally produced 'dropper' (D) which is in the process of forming a new tuber (NT) at its extremity. At a point immediately above the new tuber, the 'dropper' is always considerably swollen (B, Text-fig. 9). This region was termed the "probulb" by Morrison (1905). It is connected with the tuber itself only by a narrow neck or connective, but is usually closely applied to it, as the result of the enlargement of the tissue of the tuber (cf. Text-fig. 6).

At the end of the second season, the tuber is still fairly small, about 2 mm. in diameter, but it has been carried considerably deeper into the soil by the second 'dropper', and is thus better able to resist desiccation.

The process of progressive penetration into the soil may go on year by year, until an appropriate level has been reached. When a certain depth has been reached, however, the 'dropper' as such is no longer formed and, instead, the new tuber is developed on an extremely short stalk arising from an axillary bud immediately above the current tuber, i.e., in the same position as the 'dropper'. Thus it is situated beside, and at approximately the same level in the ground as, the current tuber. It is evident from this that the 'dropper' is simply an elongated connective, by means of which the plant is able to adjust its dormant reproductive shoot to a suitable level below the surface of the ground. The annually produced tubers are now developed as a rule at this same level.

A longitudinal section through a current and new tuber (Text-fig. 10) shows the new tuber (NT) on an extremely short connecting stalk (K), which has developed in the axil of a scale leaf just above the current tuber. Its vascular tissue arises as a branch from the bundles of the underground stem (U). In transverse section the underground stem shows a wide cortex, and a ring of vascular bundles arranged near the centre. Branches from these bundles pass through the connective and into the new tuber, where they branch again to form a ring of five or six bundles, which terminate just behind the meristem.
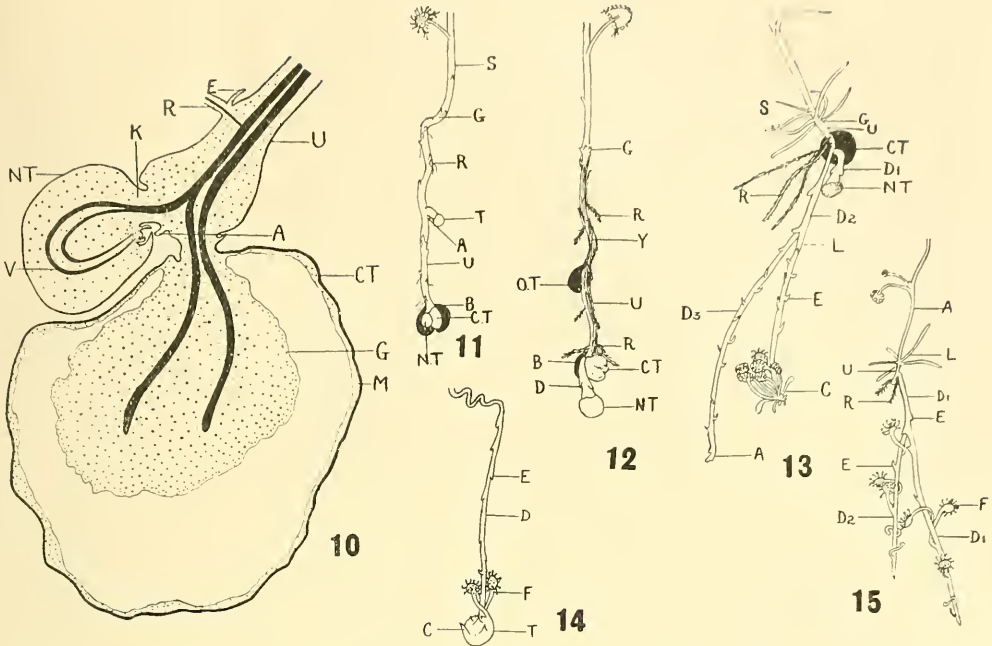
Text-fig. 10.—A longitudinal section through a current tuber showing the new tuber developing beside it. CT, current tuber; NT, new tuber; K, connective branch on which the new tuber is developed; A, scale leaf in whose axil the branch (K) arose; U, underground stem; E, scale leaf; R, adventitious root; V, vascular bundles; G, inner layers of parenchyma of the current tuber which have contracted away from the outer zone (M). × 12.

Text-fig. 11.—The underground parts of a plant of *D. peltata*. CT, current tuber; NT, new tuber; B, scales formed from the remains of old tubers; U, underground stem; T, tuber; A, scale leaf in whose axil the tuber (T) arose; G, ground level; S, aerial stem; R, adventitious roots situated at the base of the scale leaves. × 1 approx.

Text-fig. 12.—The underground parts of a plant of *D. peltata*. CT, current tuber; D, 'dropper'; NT, new tuber; B, scale formed from the remains of an old tuber; OT, an old tuber penetrated by the underground stem (U); Y, detritus formed from the fibrous remains of previous underground stems; R, roots; G, ground level. × 1 approx.

Text-fig. 13.—An abnormal development of the underground parts of *D. auriculata* which had been partially exposed to light. CT, current tuber; D_1, 'dropper' bearing a new tuber (NT); R, adventitious roots; D_2, a second 'dropper' arising on the underground stem near D_1; D_3, a 'dropper' originating as a branch of D_2; A, apical bud of D_3; C, apical bud of D_2, which is forming a cluster of foliage leaves; L, level of soil from which D_1 and D_2 were projecting; U, underground stem; E, scale leaves; S, rosette of linear scale leaves at ground level (G). × 1 approx.

Text-fig. 14.—A 'dropper' bearing an abnormal tuber of *D. auriculata*, which had been partially exposed to light. T, tuber; E, scale leaves; C, enlarged scale leaves; D, 'dropper'; F, foliage leaves which have developed on the tuber in place of scale leaves. × 1 approx.

Text-fig. 15.—An abnormal development of the underground parts of *D. peltata*. U, broken underground stem; R, roots; D_1, 'dropper'; D_2, a 'dropper' which has arisen as a branch of D_1; E, scale leaves; F, foliage leaves which have developed on the 'dropper' in place of scale leaves; L, rosette of linear scale leaves at ground level; A, aerial stem. × 1 approx.

Two of these are shown in section in Text-figure 10, at V. The connection of the bundles of the current tuber (CT) with the underground stem of the previous year is not shown in this section, since they curve upwards in a plane more or less at right angles to the direction of section.

As the new tuber increases in size the food materials in the current tuber become exhausted, and the inner tissue (G, Text-fig. 10) shrinks away from the outer layers (M). The outer zone consists of the epidermis and a few rows (about three to five) of parenchyma cells, which are torn away from the remainder of the ground tissue. As the new tuber develops, therefore, the current tuber becomes soft and pulpy. The young tuber presses in the current tuber more and more, and so comes to fill the space once occupied by it. The current tuber finally, when all its foods are exhausted, remains as a dark brown or black concave shell, adhering to one side of the newly formed tuber (B, Text-fig. 11). This process may go on at the same level for a number of years, the hardened shells of the old tubers persisting as outer protective coverings. The young tubers are formed alternately on different sides of the stem, so that a number of these black shells or scales may be found completely enclosing the current and new tubers.

Planchon (1848) tentatively compared these structures to the outer scaly leaves of the onion, while Morrison (1905) considered that they were an exfoliation of annual occurrence from the substance of the "bulb", and apparently did not realize that they were the exhausted shells of previous tubers. Their presence may explain why Morrison and others termed the perennating organ a bulb.

When the apex of the connective becomes inverted to form the new tuber, the growing point is invariably situated on the side of the new tuber against the current tuber, never towards the outside. This orientation of the apical bud causes it to be situated immediately beneath the existing underground stem. After the aerial parts have died down, this stem becomes soft and rotten, leaving only a small scar at its point of attachment with the newly formed tuber. When the growing point starts to shoot, the new stem grows directly upwards, and so penetrates through the rotting tissues of the old underground stem. It is possible that the soft central core forms a channel of least resistance to the developing shoot, which would also be protected from abrasive soil particles by the disintegrating fibrous outer layers.

It has been suggested by previous writers (see Rendle, 1925) that this dead material may function as a velamen does, in holding moisture around the underground stem. This has a strongly lignified epidermis, but the cell walls have large pits on their outer sides. This structure may allow a certain amount of water to enter the underground stem over its whole surface.

This detritus of the fibrous remains of previous underground stems can be seen on all of the older plants (Text-fig. 12), when it may be quite thick, and frequently on those of only two or three years. Sometimes the underground stem passes through the remains of old tubers (as at OT, Text-fig. 12), which may appear to belong to it, but can always be easily separated, and show no point of attachment.

The presence and cause of this detritus was noticed by Morrison (1905) in his description of the Western Australian species. It is probable, however, that when he speaks of the presence of several "bulbs" arranged one above the other, he mistook the old remains of previous tubers for functional tubers. The appear-

ance was also observed by Planchon (1848), but with the material at his disposal, he was not able to satisfy himself as to its origin and significance.

Robertson (1906) has described the 'droppers' formed by *Tulipa* and *Erythronium*, which carry the new bulb down to a suitable level in the soil, their length varying accordingly. If the bulb is already placed too deeply in the soil, the 'dropper' may be directed upwards instead of downwards, so that the new bulb develops higher than the old.

An upwardly directed 'dropper' has not been observed by the writer in any of the plants of *D. peltata* or *D. auriculata* examined. One specimen found, however (Text-fig. 11), illustrated the way in which tubers may be placed at a higher level in the ground. A tuber (T) has been formed relatively high up on the underground stem, in addition to the new tuber (NT) formed at the normal position beside the current tuber (CT).

There is typically only one 'dropper' or one young tuber produced every season by each plant. In just a few cases, however, out of the several hundred plants examined, multiplication of the underground stem had occurred to form two 'droppers' (e.g., Text-fig. 13), each able to form a tuber. Much more frequently the ascending axis branches to give two aerial stems, at about ground level, or just below the surface. This often occurs if the first shoot is injured. Examples have also been seen in which the apex of the 'dropper' had been injured, and an axillary bud of the 'dropper' had grown out and taken its place. Similarly, even in uninjured plants the 'dropper' occasionally branches (Text-figs. 13, 15).

Owing to the rapid disintegration of the old underground organs, this method of vegetative multiplication can only definitely be observed when branching has occurred during the current season. Often, however, plants are found growing in clusters of two or three, with their underground parts in close contact, and sometimes even growing up through the same fibrous material, but nowhere actually joined. It seems certain that in many cases these groups have arisen from the one plant by branching of the underground parts during a previous season, their connection having subsequently disintegrated.

The relationship between the time of appearance of the new tuber or 'dropper' and the vegetative and flowering phases of the plant has been investigated. No direct correlation could be found. Sometimes the new tuber has reached a considerable size while the aerial part of the plant is still short and with only leaf bud. At other times, even flowering plants have only an extremely small new tuber. The two processes then, of tuber and flower production, seem to go on independently of one another.

Certain abnormal specimens collected are of interest, in that they show the marked plasticity of the underground parts, and their reactions when subjected to unusual stimuli.

Several plants of *D. auriculata* were found growing on a steeply sloping rock ledge on which the soil was very shallow. Long 'droppers' had been formed, and had grown completely out of the soil. These were exhibiting some most unusual features. Text-figure 13 illustrates a typical example of the lower parts of one of these plants. The current tuber (CT) is situated only a few millimetres below the surface of the soil. A young tuber (NT) is already being formed on the end of a short 'dropper', and in addition a second 'dropper' has arisen from a bud on the underground stem close to the first, and has formed a long stolon. This in turn has given rise to a third 'dropper'. These last two 'droppers' were

free from the soil from about the level L, and were quite green in colour, in distinction from the usual white appearance. Their scale leaves had become unusually large, and were quite green. The most extraordinary feature, however, is shown at C, where the whole apical shoot of the 'dropper' has been transformed into a cluster of small foliage leaves. Every gradation between a normal foliage leaf with glands, and scale leaves can be seen. The growing point has meanwhile become inverted, as happens during tuber formation. The tuber has thus been replaced by a small plant, which, however, at this time, had no connection with the ground. The fact that several 'droppers' were produced by many of the plants, indicates that failure to reach a suitable substratum on the part of the first 'dropper' may lead to the development of other 'droppers'.

An intermediate case between these clusters of leaves, and the normal tuber, is shown in Text-figure 14. Here the tuber has been formed, but the scale leaves on it have become much enlarged, and two of them have developed into foliage leaves. This transitional stage demonstrates the plasticity of these modified leaves normally present on the 'dropper' and tuber, and establishes the fact that their scale-like form is the result of their subterranean environment.

Text-figure 15 illustrates a specimen of *D. peltata* whose behaviour has been similar to that described above in plants of *D. auriculata*. At ground level a rosette of elongated scale leaves can be seen. The 'dropper' has branched, and both 'droppers' have developed several foliage leaves with glandular hairs in place of the usual scale leaves. The underground stem had previously been injured just below ground level, and only a very small length of stem marks its former position.

Ecological.

Many plants were found which appeared to have previously reached a permanent level, having the remains of old tubers about them, and yet had sent down a 'dropper' to a still lower level during the current season. This would take place in cases where the soil had been somewhat washed away from the surface, but it also occurred in places where no sign of such a reduction of level could be detected. The tubers, also, of some of these plants were already at a considerable depth.

The relation between the depth of the tuber and the habitat, especially the type of soil in which the plants occur, has been investigated. Measurements of the underground parts of 263 plants of *D. peltata* have been made. Only those plants were measured which were considered to have reached a permanent level in the soil on account of the presence of old tubers, or of a newly formed tuber at the same depth as the current tuber.

The results are represented graphically in Text-figure 16. The numbers of plants from five different localities have been plotted against the depths at which their tubers occurred below the surface of the ground. The measurements were made of the length of the underground stem from the ground level to the top of the tuber. The diameter of the tuber was not included in the measurement, in order to minimize error due to the size of the tuber.

The absolute heights of the curves are unimportant, since the measurements for the various localities were made on different numbers of plants. Only the form of the curve and the position of its maximum point is of significance. The two small secondary maxima in the curves B and E are not thought to be of significance, but due to error on account of the small numbers used.
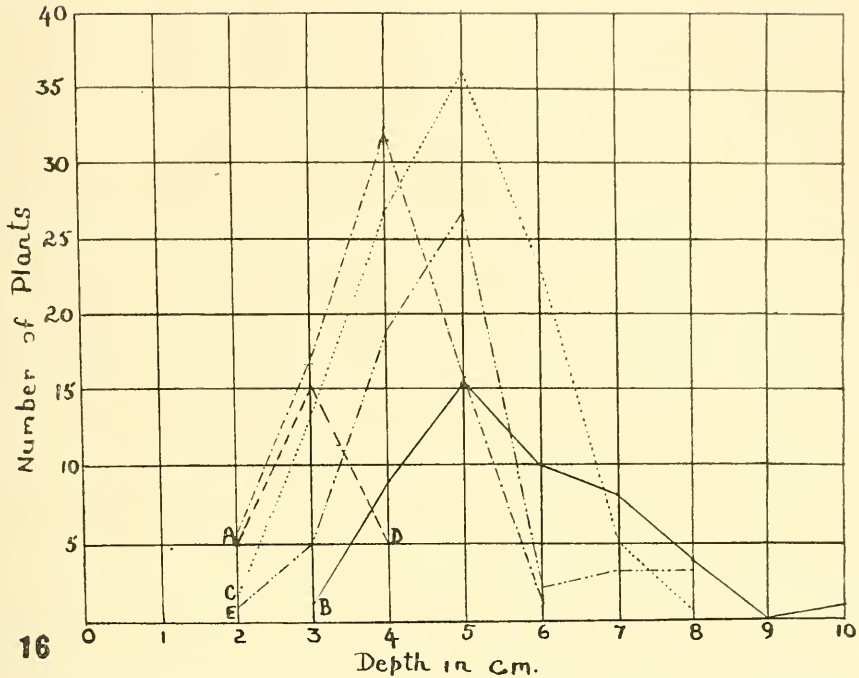
Text-fig. 16.—Graph showing variation in depth of tubers of *D. peltata* collected from five different localities. A, from Church Point, moist situation, heavy sandy soil; B, from Waterfall, rather dry situation on top of hill, light sandy soil; C, from Pennant Hills, moist situation, light sandy soil; D, from Pennant Hills, very wet situation, heavy sandy soil; E, from Pennant Hills, rather dry situation on top of hill, clay soil.

Three curves, B, C, and E, have their maximum point at 5 cm. depth in the soil, the curve A at 4 cm., and the curve D at 3 cm. This result corresponds in a general way with the moisture content of the soil that would be expected in the respective localities. The curves B, C, and E were given by plants collected from areas which would soon become dry in the hot months. The curve A was given by plants growing near a swamp on the flat top of a hill, where the soil would tend to retain its moisture much longer. The curve D is of interest in that its maximum point occurs at 3 cm. depth, since these plants were collected in a particularly moist locality which would probably not be subjected to drought during the summer months. Unfortunately this curve is based on measurements of only 20 plants, so that too much reliance cannot be placed on it.

These curves indicate therefore that the depth at which the tubers occur is influenced by habitat. The moisture relations of the soil are apparently of more significance than the soil texture, since similar curves (C and E) were obtained from plants on clay and sandy soils respectively.

The average depth of the tuber for the total number of plants examined was found to be at about 5 cm. below the surface of the ground. In the following table the numbers of plants which had their tubers at each depth from 2 to 10 cm. are given:

Depth in cm.	2	3	4	5	6	7	8	9	10
No. of plants	14	51	91	104	36	17	8	0	1

ADVENTITIOUS BUDS.
i. *Epiphyllous Buds.*

Accessory methods of vegetative reproduction have been described in various species of *Drosera*. Goebel (1913) has described a peculiar method of reproduction in *D. pygmaea*. This species produces brood buds which represent modified parts of the leaf. Proliferation of the inflorescence may also occur. Dixon (1901) recorded the production of adventitious buds borne in the angles between the pedicels and the main axis of the inflorescence. Abnormal flowers, sometimes resembling vegetative shoots, have been described by Planchon (1848), Fernald (1905) and Leavitt (1905). Levine (1916) showed that sometimes these shoots could give rise to new plants.

Epiphyllous buds in *Drosera* were probably first recorded by Naudin (1840) for *D. intermedia*. His tentative conclusion that the epidermis was ruptured, and hence that the buds originated endogenously, does not agree with the findings of later writers.

Epiphyllous shoots were recorded in *D. capensis* by Winkler (1903), and in *D. longifolia* by Kirschleger (1855). Nitschke (1860) described similar vegetative budding in *D. rotundifolia*, and this was recorded in the same species by Graves (1897), Grout (1898), Dixon (1901), Robinson (1909), and Dennis (1926).

Leavitt (1899, 1901) propagated plants of *D. binata*, *D. dichotoma* and *D. filiformis* from adventitious buds on cut leaves. Buds appeared after about three weeks on leaves placed on sphagnum. Ames (1899) commented on the possibility of propagating certain species of *Drosera* from old leaves cut from mature plants. He found that in *D. binata*, *D. filiformis*, and *D. intermedia americana*, mature leaves which fell on the sand in which the plants were growing produced adventitious buds. Goebel (1908) also obtained adventitious buds on part of a leaf of *D. binata* kept on a moist substratum.

Salisbury (1915) again recorded the occurrence of adventitious buds on the leaves of *D. rotundifolia* and *D. intermedia* on plants which had been kept in a greenhouse. He noted that the age of the parent leaf on which they occur may vary.

Other references to adventitious buds in *Drosera* are made by Godron (1878), Geisenheyer (1898), and Heinricher (1902).

As far as is known to the writer, the origin and very early stages of development of these epiphyllous buds in *Drosera* have not previously been described.

Epiphyllous buds were first observed by the present author on *D. peltata* in November, 1931, when a few plants were found on which several of the foliage leaves had developed shoots on their upper or ventral surfaces. Some of these were miniature aerial shoots with a short axis up to 5 mm. in length, bearing small orbicular foliage leaves. Others appeared as white stolons growing vertically downwards, suggesting at once the 'droppers' of the ordinary plant. Some of the leaves bore more than one shoot. The parent laminae on which the shoots occurred were all withered at the time when they were collected. Just previous to their discovery, there had been a heavy rainfall, and the winter had been a

wet one. Similar shoots were found a few days later on plants growing on sheltered mossy rocks on the side of a hill, which were kept constantly saturated throughout the winter by water draining from the ridge above.

Subsequently it was found that these buds could be readily produced under laboratory conditions, either on leaves detached from the plant, or on uninjured plants, and thus a constant supply of material for histological examination was easily procurable.

Epiphyllous buds have been induced in the laboratory on leaves of *D. peltata*, *D. auriculata*, *D. spathulata* Labill., *D. Arcturi* Hook., and *D. binata* Labill. The last three species have buds resembling those already described by earlier writers. *D. peltata* and *D. auriculata*, however, are unlike those previously recorded in that sooner or later a 'dropper' is developed which bears the young tuber, and establishes the plant in the ground.

The following description of adventitious buds is given from a detailed examination of only *D. peltata* and *D. auriculata*, but it has been observed that the buds of *D. spathulata*, *D. Arcturi* and *D. binata* have a similar origin and early development.

Morphology.

It will be convenient to describe here the typical arrangement of the glands on the laminae. This is found to be practically the same in both *D. peltata* and *D. auriculata*. The petiole is attached to the lamina on the dorsal surface at approximately the centre of the leaf in the adult form of foliage. When the lower leaves are arranged in a rosette, however, their petioles are attached to the margins of the leaves and the laminae are more orbicular or semi-orbicular in shape. A similar shape, usually orbicular, is observed in the leaves of seedlings or young epiphyllous plants (Text-figs. 4 and 9).

In the adult foliage the whole margin is bordered by long glandular hairs. Two rows of long stalked glands, an outer and an inner, can be made out at the margin (Text-fig. 17). Approaching the centre, these are succeeded by a third row of much shorter glands, whose stalks, however, are rather longer than the remainder of the glands which occupy the central portion of the leaf and have only very short stalks. At the two angles of the adult leaf, a number of the long glandular hairs are united for part of their length to form the 'auricles'. These are particularly conspicuous in *D. auriculata* (Text-fig. 21).

Detached leaves kept in the laboratory on wet sand, or floating in water in Petri dishes, were examined at frequent intervals, in order to detect the first outward signs of bud formation. It was found that the bud arises as a swelling on the upper surface and appears to surround one of the glands completely. In Text-figure 17 a short gland can be seen emerging from the top of each of the two very young buds, so that they form swollen enlarged bases to these glands. At a slightly later stage (Text-figs. 18, 19) the gland is pushed to one side, while the bud develops a conspicuous apex and continues its growth.

Most frequently this occurs on one of the short glands situated towards the central portion of the lamina (Text-fig. 18), but occasionally one of the glands belonging to the inner or even the outer row of marginal glands gives rise to a bud (Text-fig. 19). In every case, bud formation is associated with a glandular hair, and consequently shoots always appear on the upper surface.

Only one example has been seen in which the bud appeared, from a superficial examination, to arise on the lower side of the leaf (B, Text-fig. 20). This
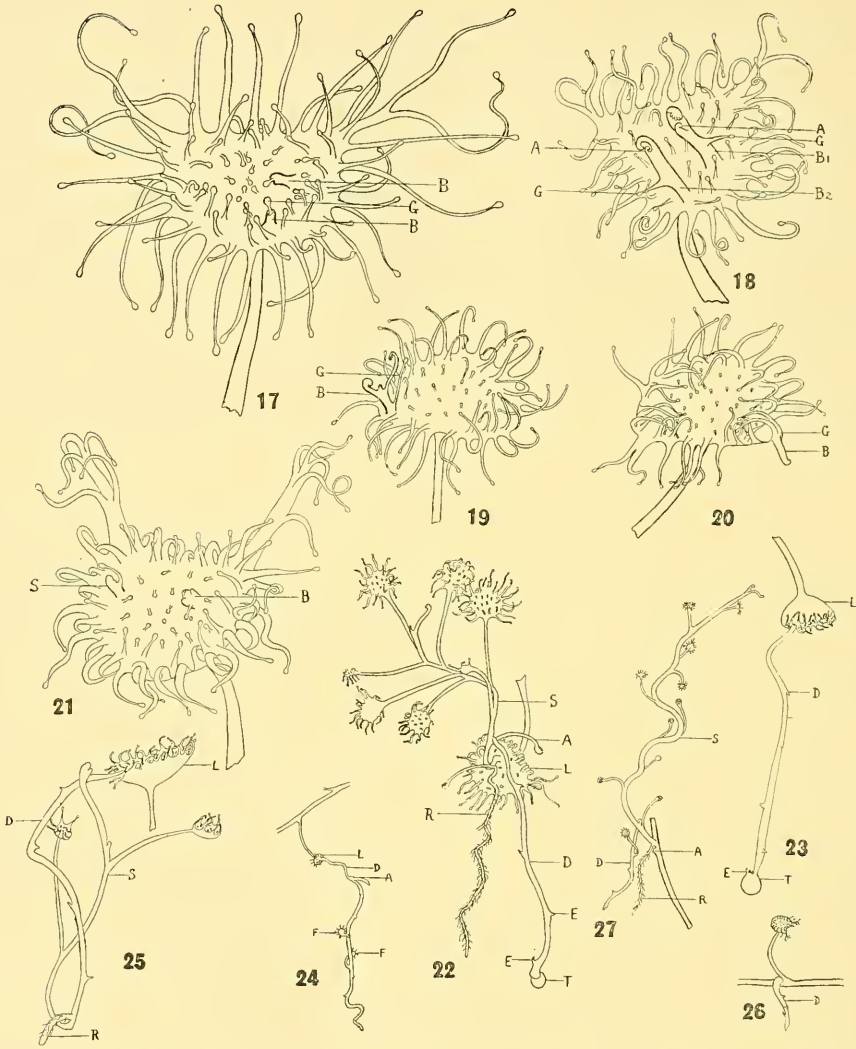
Text-fig. 17.—A leaf of *D. peltata* bearing two very young epiphyllous buds. B, buds; G, glandular hair at whose base the bud arose. × 10.

Text-fig. 18.—A leaf of *D. peltata* bearing two young epiphyllous buds. B_1 and B_2, buds; G, glandular hairs pushed aside by the growth of the buds; A, apical bud. × 10.

Text-fig. 19.—A rather juvenile shaped leaf of *D. peltata* bearing a bud (B) which has developed from the base of a long stalked gland (G) of the inner marginal row. The central short glands were withered at this stage. × 6.

Text-fig. 20.—A leaf of *D. peltata* bearing a bud (B) apparently on the lower surface. This bud has developed at the base of the fused gland stalks (G), and has grown towards the lower surface of the leaf. × 9.

Text-fig. 21.—A leaf of *D. auriculata* bearing two epiphyllous buds. S, a slender type of bud; B, a thick bud with short protuberances near its apex. × 8·5.

bud arose from the base of the fused gland stalks of the 'auricle'. The gland stalk is always ultimately pushed aside by the developing bud, and in this case it was pushed towards the centre, thus causing the bud to appear on the lower surface.

The buds are sometimes very slender from their earliest appearance (Text-fig. 18, and at S, Text-fig. 21); at other times they are quite thick with small protuberances probably representing leaf rudiments (B, Text-fig. 21). Development is similar in each case, and the forms cannot be correlated with the types of buds to be described later.

More than one bud frequently occurs on the lamina. As many as four shoots have been observed to develop and attain considerable size on the one leaf. An examination of transverse sections of leaves which have produced one or more visible buds, has led to the conclusion that any glandular hair, the cells of whose stalk are in a healthy condition, is potentially capable of giving rise to an adventitious bud. It is only on healthy leaves, therefore, that buds can be produced. The withered appearance of the lamina bearing well-developed buds, that has often been observed, is due to death subsequent to the formation of the buds. Transverse sections of the leaf often show that numerous gland stalks have been stimulated, and show early stages of division to form a meristem. It is probable that one or more meristems, slightly in advance of the remainder, or with a better food supply, become dominant and inhibit the development of other meristems.

Two types of buds may occur on the laminae in both species. These cannot be distinguished until they are about 1 to 2 mm. in length, when they assume a distinct appearance and habit of growth. The first type resembles in miniature the aerial shoot of the parent, and is, in all essentials, during the early stages of its development, similar to those figured by Naudin (1840) and others (Text-fig. 22). It has an ascending axis on which the small foliage leaves are borne. These are more or less orbicular, and resemble the leaves first borne by the seedling. Eventually an axillary bud grows out from the axil of one of these leaves, and turns downwards to form a 'dropper' (Text-fig. 22), similar in all respects to that which is produced by a seedling. This occurred after one or two months in buds grown in the laboratory. The 'dropper' usually grows over

Text-fig. 22.—An older epiphyllous bud on a leaf of *D. peltata*. L, withered parent lamina on which the bud developed; S, shoot of the epiphyllous bud; D, 'dropper' developed from a bud in the axil of a leaf (A); R, root arising near the base of the shoot; E, scale leaves; T, tuber. × 2·8.

Text-fig. 23.—An epiphyllous bud which has developed directly into a 'dropper' (D). E, scale leaves; T, tuber. × 4.

Text-fig. 24.—An epiphyllous 'dropper' bud (D) which has developed on the parent leaf (L) while it was still attached to the plant. The 'dropper' has branched at A. Foliage leaves (F) have developed where the 'dropper' was exposed to light. × 1.

Text-fig. 25.—A 'dropper' bud (D) which has arisen on the parent leaf (L). Its apex has become inverted and given rise directly to an aerial shoot (S) without the formation of a tuber. R, an adventitious root. × 2·5.

Text-fig. 26.—An axillary bud of *D. peltata* which has formed a 'dropper' (D) directly. × 1.

Text-fig. 27.—An axillary bud of *D. peltata* which has formed a leafy shoot (S). D, a 'dropper' which has developed from an axillary bud of this shoot. R, an adventitious root arising near the base of the shoot; A, leaf scar of the axillant leaf; O, part of the stem of the parent plant. × 1.

the side of the parent leaf, or occasionally forces its way through the tissue of the lamina. The 'dropper' may grow one or more centimetres in length and, on entering the ground, a small tuber is formed (T in Text-fig. 22). When this has occurred, the adventitious shoot may be considered to have become established as a separate entity, and is now in the same condition as a seedling plant is at the end of its first season.

The second type of bud differs from the first in that the apex of the bud itself becomes a 'dropper' at once, and commences to grow straight downwards towards the soil or substratum, without forming any aerial shoot (Text-figs. 23, 24). The 'dropper' is usually whitish in colour or a very pale green. If it is exposed to light for some time, as occurs when the parent leaf is some distance from the ground, the 'dropper' turns a stronger green, and the scale leaves sometimes develop as foliage leaves (Text-fig. 24). Similarly, foliage leaves are sometimes seen on 'droppers' developed on the leafy type of shoot. In some cases the 'dropper' has been seen to grow 4 or 5 cm. long (Plate viii, fig. 2), when the lamina on which the bud arose was situated at some distance above the ground, and in this case it is usually extremely slender. In a few cases when the 'dropper' was unable to reach the substratum, the apex became inverted and gave rise directly to a small leafy shoot (Text-fig. 25).

Roots were not developed under laboratory conditions until about two months after the buds had been produced. It was then found that the leafy type of buds had produced a typical adventitious root with numerous root hairs from their stems, at a point just above their connection with the parent laminae. If the root occurred rather higher up on the stem, it was found that it had developed just at the base of one of the first leaves (R, Text-fig. 22). At the time when roots are first noticeable, the parent lamina is always very withered. No roots were ever found on the 'dropper' buds, except in the rather unusual case shown in Text-figure 25, where the 'dropper' apex had turned to form a leaf shoot. In this case a root occurred at about the point where its direction of growth had changed.

ii. *Axillary Shoots.*

Normal buds present in the axils of the foliage leaves on the aerial stem have occasionally been observed to give rise to new plants. Under ordinary circumstances the dormant axillary bud is extremely small and insignificant, no elaborate shoot being organized. A 'dropper' may either arise directly from the apex of an axillary bud (Text-fig. 26), or else the axillary bud may produce an ordinary leafy branch, and a 'dropper' may develop from one of the axillary buds of this branch (Text-fig. 27).

HISTOLOGY OF EPIPHYLLOUS BUDS.

Leaves showing very young stages of adventitious bud formation were embedded and microtome sections cut. The material was fixed either in acetic alcohol or in Flemming's strong fixative, and the majority of the sections were cut at 10μ and mounted serially. Safranin and Delafield's Hæmatoxylin were the chief stains used.

The meristem forming the bud was found to arise from adult cells at the base of a glandular hair, both in the mesophyll of the leaf, and the epidermal cells of the upper surface. Sections were cut of fresh leaves just brought into the laboratory, and of detached leaves which had been kept in water for varying

intervals. It was found that the earliest stage in the appearance of a meristem could first be detected after about eight days in water.

Text-figure 28 shows a longitudinal section of an adult gland prior to any meristem formation. An adequate description of the gland in *D. rotundifolia* has been given by Huie (1896) as well as by previous investigators, and the glands of *D. peltata* and *D. auriculata* have the same structure.

The earliest stage in regeneration that could be definitely detected is shown in Text-figure 29. A few cells of the mesophyll of the leaf, near the base of the gland, are seen to have divided at A, and a few cells of the epidermis (B) also show signs of recent divisions. At this stage the mesophyll and epidermal cells are highly vacuolated, with only a thin layer of cytoplasm lining the walls.
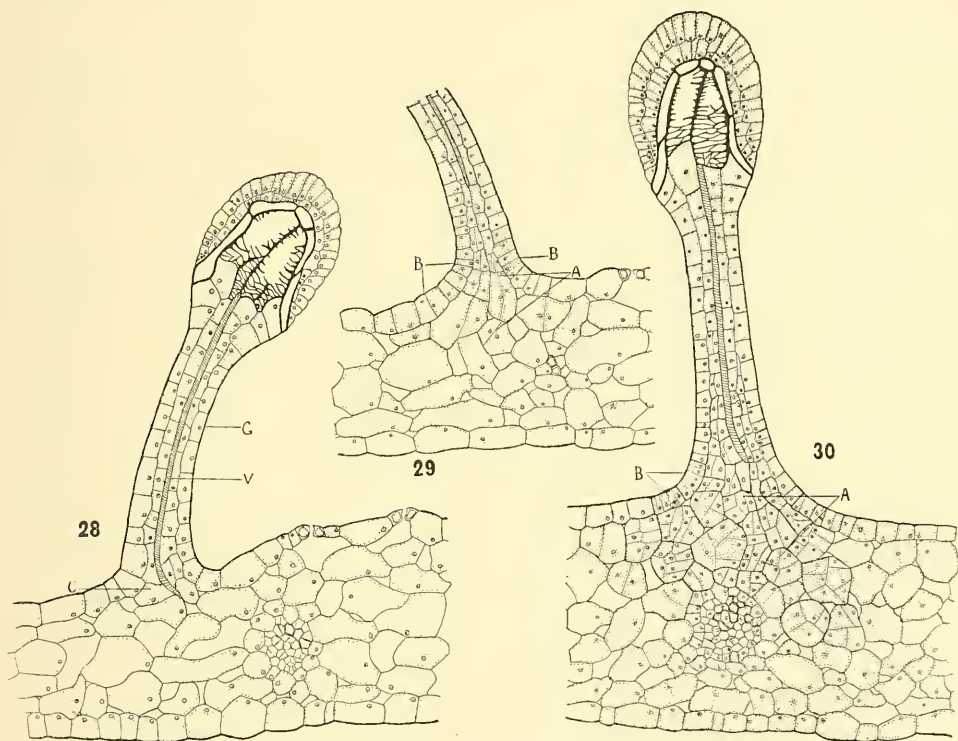
Text-fig. 28.—A longitudinal section through a mature glandular hair (G), and transverse section through the lamina. V, spiral vessel which passes up through the stalk of the gland; C, vacuolated cells at the base of the gland. × 150.

Text-fig. 29.—A transverse section of a leaf at the base of a gland showing the first divisions of the cells to form a bud, in the mesophyll (A) and epidermal cells (B). × 150.

Text-fig. 30.—A transverse section of a leaf and longitudinal section through a gland showing divisions in the mesophyll (A) and epidermal cells (B) at the base of the gland. The cells are becoming rather more densely cytoplasmic, and the original cell walls can be distinguished from those recently formed. × 150.

K

Text-figure 30 shows an interesting stage in the development of the bud. The mesophyll cells (A) at the base of the gland now show numerous divisions, and the epidermal cells (B) have also undergone several divisions. The difference in thickness between the old cell walls of the mesophyll cells, which have secondary lamellae, and the primary walls of the newly formed cells is clearly marked at this stage. It will be observed, therefore, that each mesophyll cell and certain of the epidermal cells immediately at the base of the gland are forming meristems within themselves.

At the stages shown in Text-figures 28 and 29 the intercellular spaces are large and conspicuous throughout the mesophyll. At the stage shown in Text-figure 30 they are becoming quite small and inconspicuous in the region of the meristem. At this stage the cells of the developing meristem are still fairly highly vacuolated, though certain of the epidermal cells are becoming rather more densely cytoplasmic.

At a still later stage a slight protuberance of the leaf surface becomes evident at the base of the gland (Text-fig. 31), especially on one side (P), so that the gland stalk is being very slightly pushed to one side. The old walls of the original mesophyll cells can still be clearly detected in some places (M), but their complete original outlines cannot now be traced. The exact fate of these cell walls is uncertain.

Text-figure 32 shows a still later condition. At this stage the bud could be detected as a small protuberance on the leaf, by means of a hand lens. The stalk of the gland (G) is situated near the top of the bud, but now definitely over to one side of it. The meristematic activity has become concentrated on one side of the gland stalk (M), and this now grows forward carrying the gland with it for a short time (cf. Text-figs. 18 and 19).

A tangential section of a well developed bud (Text-fig. 33) shows the gland still attached some distance up the stalk of the bud. It is usually difficult to obtain a section through an older bud which is median through its meristematic apex, and also includes the stalk and head of the gland at whose base it arose. This is because the gland is frequently situated at the side of the growing bud and at right angles to the plane in which the first leaf is developed. A median longitudinal section through a similar bud shows that the meristematic apex is now clearly differentiated, and is giving rise to leaf primordia (Text-fig. 34).

Dixon (1901) and Salisbury (1915) state that the epiphyllous bud is in vascular continuity with the parent leaf. On the other hand, Winkler (1903) and Robinson (1909) state that these adventitious buds are not connected with the vascular system of the parent plant.

A single spiral vessel passes down the stalk of the glandular hair. This connects the group of tracheides situated in the head of the gland with the vascular tissue of the leaf, and thus supplies the glandular tissue with water. This vessel is invariably in connection with one of the vascular bundles of the leaf, though the ultimate ramifications of the veins may be sometimes too fine to trace to each gland if the whole leaf be examined externally. Even in transverse section of the leaf, since the vein may be almost parallel to the direction of section, it is occasionally difficult to demonstrate the actual connection unless serial sections are carefully examined. The presence of this vessel makes it apparent that the bud is provided with a rudimentary vascular tissue from the beginning of its development. Vascular tissue is subsequently differentiated

behind the growing apex in the usual fashion. At V in Text-figure 34 the central cells behind the meristem are becoming elongated to form conducting cells. That the vascular system of the bud is continuous with that of the parent lamina is also shown in Text-figures 32 and 33.
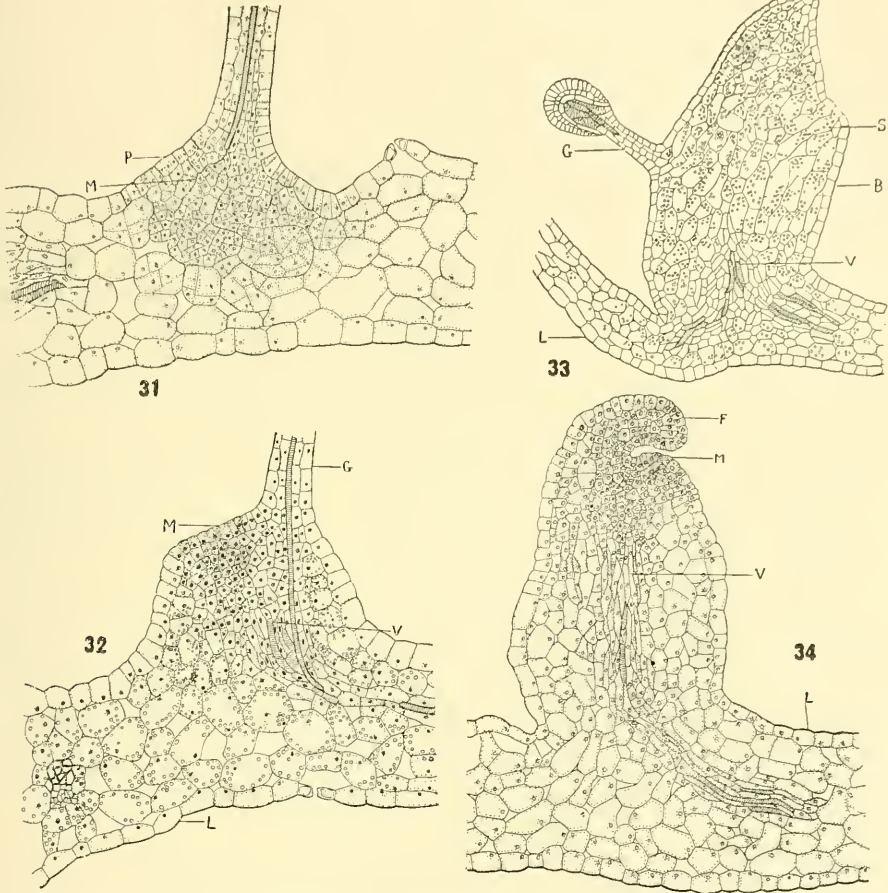
Text-fig. 31.—A later stage in the development of a meristem. Outlines of the original cell walls can be seen, as at P, and M, but the identity of the original cells is becoming lost. The cells are now fairly densely cytoplasmic. The upper surface of the leaf is protruding slightly, as at P. × 150.

Text-fig. 32.—A longitudinal section through a young epiphyllous bud. The growing point (M) is now situated at one side of the gland stalk (G). V, vascular tissue being formed behind the meristem; L, parent lamina. × 150.

Text-fig. 33.—A tangential longitudinal section through a bud (B) showing the glandular hair (G) still attached at some distance up its stem. The vascular tissue (V) of the bud is connected with that of the parent leaf (L). Starch grains (S) are present in the cortical cells of the bud, and in the mesophyll cells of the parent lamina near the bud. × 60.

Text-fig. 34.—A median longitudinal section through a bud. M, apical meristem; F, first leaf of bud; V, cells behind the growing point differentiating to form vascular tissue. The vascular tissue of the bud is in continuity with that of the parent leaf (L). × 123.

Salisbury (1915) stated that the buds that he examined were always situated close to the main vein of the leaf, with which their vascular tissue was at first connected. In the present investigation, however, it has been found that, in *D. peltata* and *D. auriculata*, the buds may be connected also with any of the minor veins of the leaf.

The problem of regeneration of plant cells is one of considerable interest. Several authors, e.g., Goebel (1903), include in the term regeneration those cases in which new organs arise from the development of latent root and shoot primordia. In most cuttings the shoot will arise from an axillary bud if one is present. To this class also would belong those plants in which new organs arise from the cambium in cuttings, since the primordia initiating their growth definitely arise from previously existing meristematic cells. In *Bryophyllum calycinum*, Naylor (1932) has shown that dormant primordia occur in the notches of the leaf throughout its life, and that regeneration occurs from these primordia when the leaf is detached from the plant.

In many plants also, adventitious shoots may occur from the ends of petioles of leaf cuttings, and propagation may be carried out in this manner. A general account of the literature on the production of buds on roots and leaves is given by Holm (1925). The term regeneration may be more strictly applied to that class of phenomena in which the development of new organs is initiated by cells which have previously undergone vacuolation, and hence have reached what may be termed the adult condition. This type of regeneration is less common in the higher plants. In the propagation of *Begonia*, however, shoots may arise near the cut veins from the callus which is formed over the wound, or, in certain cases, they are developed by the division of a group of epidermal cells, as recorded by Hansen (1881).

In the discussion on the origin of the adventitious buds in *Drosera* it has been shown that the first divisions occur in cells which are in a highly vacuolated condition, similar to a mature non-dividing parenchyma cell, and that the cytoplasm becomes progressively more dense during subsequent divisions. *Drosera*, therefore, exhibits a similar type of regenerative phenomena to that shown by *Begonia*. There is no sign of any dormant meristematic cells in the leaf which could give rise to shoots, as there are in the leaf of *Bryophyllum*. The cells which divide first are mesophyll and epidermal cells and are in no way connected with a cambium.

Physiology of Epiphyllous Buds.

The food materials stored in the leaves of *Drosera* were investigated with the view of detecting any differences which might occur between ordinary fresh leaves and leaves which bore adventitious buds.

All leaves which had been freshly collected, or had been kept in a fairly light position in the laboratory, gave a strong starch reaction with iodine. This starch may be present in two forms. Granules can be seen within the chloroplast, often two or three grains occupying almost the whole volume of the chloroplast. Chloroplasts occur in the epidermal cells of the leaf in *D. peltata* and *D. auriculata*, as in other species of *Drosera* (Solereder, 1908), though they are less plentiful there than in the cells of the mesophyll.

Starch also occurs as free grains. This is the form in which it is stored in the tuber, and it is usually plentiful in the 'dropper', but it is not very abundant in the fresh leaf. A little may often be seen in cells close to the vascular bundles.

When an adventitious bud arises, however, the cells in its vicinity become a centre of carbohydrate concentration, and numerous grains of starch are found in them (Text-fig. 32). As development of the bud proceeds, this starch is apparently transferred to its tissues, where it is stored in small grains in the cortex (Text-fig. 33). This abundance of starch in the developing bud was also noted by Salisbury (1915). No starch reaction was given by leaves which had been kept in darkness for 24 hours or longer.

A slight tannin reaction was shown by the contents of the cells of the gland stalk and head when tested with ferric chloride.

Fat was found to be very plentiful in almost all of the leaves examined. It is found in the cells of the gland heads, in the epidermal cells of their stalks, and throughout the epidermis of the lamina. Occasional cells of the mesophyll also contain it, especially those near the veins. In the epidermal cells of the long stalks of the marginal glands, it occurs in large globules up to 20μ in diameter. In other cells it may be in globules varying from a similar size to such small particles that, under relatively low magnification, it appears to be diffused throughout the cytoplasm.

This fat can be readily demonstrated in fresh sections with osmic acid, with which it immediately stains black. It is readily soluble in alcohol, as well as in the usual fat solvents such as chloroform and ether. It appears to be in two forms in the leaf. That in the epidermis of the smaller glands is soluble in chrom-acetic fixative, so that leaves fixed in Flemming's strong fixative (osmic acid, chromic acid and acetic acid) did not show fat in the epidermis when subsequently sectioned, although they appeared dark in colour. The large globules of fat in the long stalks of the marginal glands did not dissolve in Flemming's fixative. The fat gives a blue colour with Nile Blue Sulphate, suggesting that it is of the nature of a fatty acid. A rather lighter fat reaction was given by plants which had been kept in the laboratory for more than nine months, and whose present shoot had arisen from the tuber while in a covered glass dish. This may have been due to the effect on their metabolism of the unnatural conditions in which they were growing, or it may possibly be associated with their inability to capture and digest insects. Darwin (1878) showed that plants of *D. rotundifolia* which were allowed to capture insects, or were fed on small pieces of meat, became more vigorous in their growth than plants which were not supplied with organic material.

Certain other bodies appear in some cells of the leaves and other parts of the plant body, whose nature and origin could not be definitely established. These appear as spherical globules, varying in size up to about 10μ. They are usually single, but sometimes in clusters as though they were in contact, suggesting that they are in at least a semi-solid state. The larger bodies are black in colour, or an olive-green in thin microtome sections. Many of the smaller ones appear reddish-brown, but they are thought to be all of a similar nature.

These bodies do not change colour with osmic acid, and are insoluble in alcohol, chloroform, ether, or dilute or concentrated hydrochloric acid. On account of their strong natural colour, few tests involving colour reactions could be used. With Nile Blue Sulphate they stained blue in thin section. It is thought that they are probably hydrocarbons formed during the metabolism of the fats, especially since they occur chiefly in the epidermis where the fats are most abundant. The possibility that they represent decomposition products is suggested

by the fact that they were found much more abundantly in leaves which had become withered and were being attacked by saprophytic fungi under the humid conditions prevailing in the laboratory experiments. They are not invariably present, as sections of some leaves did not show any of these bodies.

It has been observed by several previous writers (Grout, 1898; Graves, 1897; and Salisbury, 1915) on the epiphyllous buds of *Drosera*, that their production appears to be associated with very moist conditions. Dixon (1901) asserts, on the other hand, that adventitious buds appear only when the plant is allowed to dry out. He states that they were produced within two months on plants, growing on sphagnum under a bell-glass, which were allowed to dry out. It seems to the present writer, however, as far as can be judged from his brief description, that the atmosphere under the bell-glass would become extremely humid. Under such conditions, it has been found in the present investigation, buds may be detected after 14 days on some leaves.

A number of experiments have been carried out on *D. peltata* in an endeavour to ascertain the nature of the stimuli which cause or permit the regeneration of tissue, and hence the development of the buds. The results of these are summarized below.

It was found early in the present investigation that abundant moisture favoured the production of epiphyllous buds. In the field they have only been found in extremely wet situations. They are produced readily on the leaves of plants kept in glass dishes with bell-covers in the laboratory, though their appearance under these conditions is rather slower than when the leaves are detached from the plant. Plate viii, figures 1 and 2, shows buds on plants kept under these conditions. Numerous buds appear, after two or three weeks, on detached leaves (laminae and petioles) placed on wet sand, or floating on water. In the latter case, often 50% or more of the leaves could be induced to produce buds.

When stem cuttings including at least one node and leaf were placed under moist conditions, usually an axillary bud grew out and formed an aerial shoot. Occasionally an epiphyllous bud was produced. In *Begonia* and *Bryophyllum*, epiphyllous buds are not usually produced if an axillary bud is present. It is rather surprising, therefore, that in *D. peltata* epiphyllous buds are so readily produced on complete plants.

Leaves which had been injured, e.g., by the removal of a few gland heads, were still able to produce buds, but these always arose from an uninjured gland, away from the injured part.

Ames (1899) stated that a low temperature was favourable to the production of buds. In *D. peltata* it has been found that variation of temperature does not appear to have any noticeable effect within the limits experienced in the laboratory, i.e., between about 12° and 26° C. No controlled experiments were carried out to test this factor, but buds occurred equally well during the early summer and the middle of the winter.

The buds are produced most readily in fairly bright light. Leaves placed in darkness or in deep shade did not show any signs of regeneration.

Leaves fed with minute pieces of meat became contaminated with bacteria and had to be discarded. It is unlikely, however, that the metabolism associated with insect digestion is necessary for bud production, since young leaves which opened under cover in the laboratory frequently formed buds. Leaves fed by placing in a 2% solution of glucose produced no buds, but turned a deep red colour, and their glands all became bent towards the centre of the leaf.

Buds most frequently arise on leaves of the typical adult form, but occasionally they are noticed on the more orbicular shaped leaf characteristic of the rosette leaves. In order to test whether the older or younger leaves produced buds more readily, leaves were detached from 40 plants and placed on wet sand in the order in which they occurred on the plant, all living leaves being included. It was found that the highest proportion of buds occurred in the upper third of the plant. The middle leaves produced fewer buds, but were in turn more productive than those belonging to the lower third of the plant. This result can be directly correlated with the healthy appearance of the glands on the leaves, since the glands of the lowest leaves are often slightly withered when the leaf is still living. On the other hand, young leaves near the apex, which were only just unfolding, frequently produced buds.

The only factor, therefore, which can be definitely stated to be essential for bud production is that of abundant moisture. Very humid conditions, with consequent reduction of transpiration, favour the initiation of a meristem.

Summary.

D. peltata and *D. auriculata* are winter herbs common in the Sydney district. They perennate by means of subterranean tubers which occur at the base of underground stems.

The annual development of the tubers on the plant is described, commencing from the germination of the seed. A 'dropper' arises from an axillary bud of the seedling, and penetrates for a short distance into the ground. A tuber develops at its apex by an inversion of the growing point and an enlargement of the cortical tissues. The next season's shoot arises from this tuber. A 'dropper' may be formed each season for several years, until the tuber is situated several centimetres below the surface of the ground. After this, the new tuber is formed at the same level as the current tuber each season.

The shoot developing from the tuber at the beginning of the season penetrates through the remains of the old underground stem, which persists as a loose fibrous sheath around it. The 'dropper' and the underground stem bear small colourless scale leaves. The underground stem bears a number of short adventitious roots, densely covered with root hairs.

Several abnormal specimens are described which illustrate the plasticity of the underground parts. If exposed to light, foliage leaves may develop on the 'dropper' in place of scale leaves.

Branching of the 'dropper' may occur, resulting in the formation of two tubers. Sometimes a second tuber may be formed from a bud on the underground stem some distance above the current tuber.

The relation between the depth of the tuber and its habitat is considered. A variation diagram is given for several localities, which illustrates the effect of habitat on the depth at which the tuber is placed when a permanent level has been reached by means of the 'droppers'.

Accessory methods of vegetative reproduction are described. Axillary buds on the aerial stem may occasionally give rise to a 'dropper', or to a leafy shoot on which ultimately a 'dropper' develops from an axillary bud. An adventitious root develops at the base of the stem of the leafy type of bud after about two months.

The epiphyllous buds originate by the division of adult vacuolated cells situated immediately at the base of a glandular hair. These become meristematic and the bud grows up, pushing the gland to one side. The vascular tissue of

the bud is in continuity with that of the parent lamina. Starch accumulates in the leaf in the vicinity of the bud, and passes into the cortical cells of the bud.
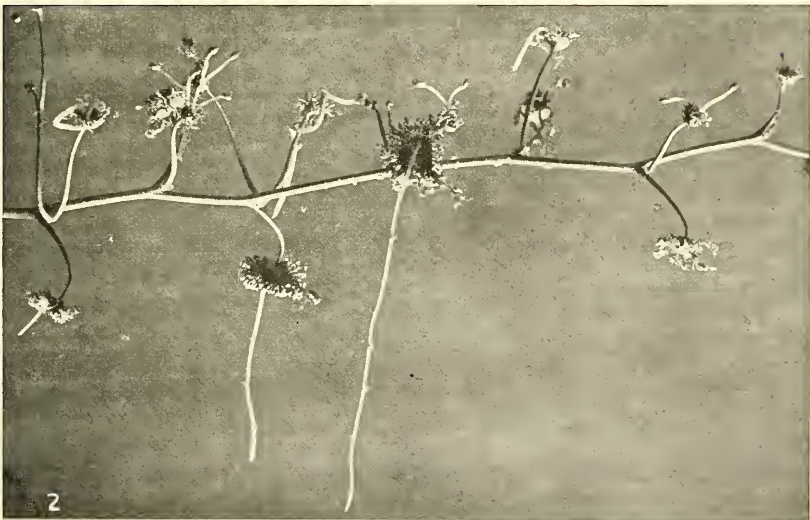
Epiphyllous buds arise either on detached or undetached leaves when placed in very moist conditions.

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* These papers were not available to the author.

Drosera peltata.